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Interrelationships of Fossil and Recent Anchovies (Teleostei: Engrauloidea) and Description of a New Species from the Miocene of Cyprus

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ABSTRACT

Aside from species described only from otoliths, there are six alleged species of fossil anchovies (Engrauloidea). Of these only one (†*Engraulis macrocephalus* from the Plio-Pleistocene of Italy) is recognizable as an anchovy on the basis of character information. Two are recognizable as clupeomorphs and probably as clupeids (†*Engraulis longipinnis*, †*Stolephorus lemoinei*). Three are unrecognizable as clupeomorphs (†*Engraulis evolans*, †*E. brevipinnis*, †*Engraulites remifer*). A new (and only the second valid) fossil species of anchovy, †*Engraulis tethensis* n. sp. from the Upper Miocene of Cyprus, is the oldest known species of the group. The scarcity of fossil anchovies is anomalous in view of their abundance today (at least 130 species) and the abundance of fossil herrings (well over 100 species). Interrelationships of clupeomorph subgroups imply that anchovies (Engrauloidea) are as old as herrings (Clupeoidea). Ecology may explain the scarcity of fossil anchovies.

INTRODUCTION

Anchovies (Engrauloidea) are a large group of clupeomorph fishes that in the Recent fauna includes about 15 genera and 130 species. Although anchovies are most diverse in the tropics (Hildebrand, 1964), they are found in temperate regions throughout the world. Most anchovies are inshore marine fishes, but several species migrate up rivers, and some live permanently in fresh water. Most anchovies are small planktivorous carnivores, although one species reaches 37 cm or more (Roberts, 1978, p. 29). Anchovies are extremely abundant. In spite of their small size (usually less than 15 cm), they are among the most important commercial fishes. Their great abundance and taxonomic diversity, and ap-

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parently great age (at least as old as mid-Paleocene, according to phylogenetic studies) make the scarcity of fossil anchovies anomalous. The systematics of Recent anchovies will be discussed below, followed by a review of the fossil species and a discussion of the scarcity of fossil anchovies.

Acknowledgments

For the loan of specimens, we thank Drs. Daniel Goujet (MNHN), Colin Patterson (BMNH), and Peter U. Rodda (CAS). We thank Dr. Heinz Kollman (NMWGPA) for sending us the photographs used in figure 8 and Dr. Daniel Goujet for use of the photographs in figure 6. Dr. Lorenzo Sorbini (Museo Civico di Storia Naturale, Verona) helped us locate the types for †*Engraulis brevipinnis* Heckel and †*E. longipinnis* Heckel. We also thank Dr. Colin Patterson for allowing us to describe the new species of fossil anchovy below.

Methods

The clupeomorph classification used here follows Grande (1985). Preural vertebrae were counted anteriorly from the anteriormost vertebra, bearing the first neural spine, back to preural 1 (the centrum bearing the parhypural). Counts of dorsal and anal fin pterygiophores (proximal radials) include the last modified element (the "stay" of Weitzman, 1962, and others). All other counts and measurements follow Grande (1985). For *Engraulis encrasicolus* (tables 1 and 2), meristic and morphometric data were collected on samples of 20 and 10 specimens, 50–70 mm sl (AMNH 44411, Lebanon, St. George Bay).

The names of all fossil taxa mentioned in text are preceded by a dagger (†). Actual specimens of all cataloged specimens mentioned here were examined except for the NMWGPA material, which was examined on the basis of detailed photographs.

Abbreviations

INSTITUTIONAL

AMNH, American Museum of Natural History, New York
BMNH, British Museum (Natural History), London
CAS, California Academy of Sciences, San Francisco
MNHN, Museum National d'Histoire Naturelle, Paris
NMWGPA, Naturhistorisches Museum Wien Geologisch—Palaontologische Abteilung, Burgring, Vienna

ANATOMICAL

aa, anguloarticular
de, dentary
ep, epural
hm, hyomandibular
hs, hemal spine
hyp, hypural
iop, interopercle
mx, maxilla
np, neural plate (modified neural spine)
ns, neural spine
op, opercle
ph, parhypural
pop, preopercle
pu, preural vertebra
q, quadrate
r, retroarticular
sop, subopercle
u, ural vertebra
un, uroneural

RECENT ENGRAULOIDEA

Systematics: Traditionally (fig. 1), anchovies have been placed within a subdivision (Clupeoidei) of an order or superorder of teleostean fishes (such as Isospondyli, Clupeiformes, or Clupeomorpha), together with one or more families of herrings, such as Pristigasteridae, Chirocentridae, etc. (Jordan, 1923; Svetovidov, 1952; Whitehead, 1968; Nelson, 1970; Grande, 1985).

Anchovies are currently recognized as members of the group Clupeomorpha (herring-like fishes), as evidenced by several characters unique to that group. One character is an otophysic connection by way of a paired diverticulum of the swimbladder that penetrates the exoccipital bone of the skull, extends into the prootic bone, and forms ossified bullae in the prootic and pterotic bones. Anchovies have also a recessus lateralis, a unique type of abdominal scute, and several

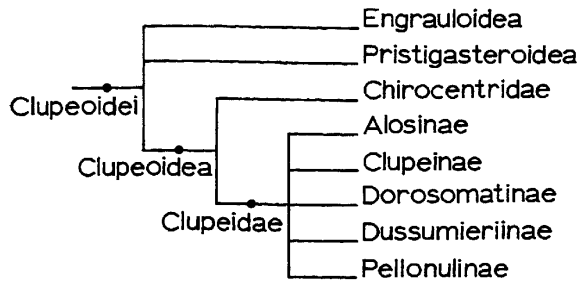

FIG. 1. Clupeoid phylogeny, after Grande, 1985.

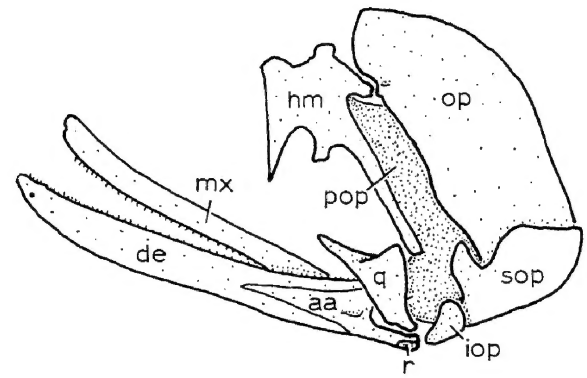

FIG. 2. Medial surface of jaws, suspensorium (in part) and opercular bones; drawn from specimen in figure 3A (*Engraulis guineensis*), showing orientation of quadrate and hyomandibular bones.

other characters found only among clupeomorphs.

DIAGNOSTIC CHARACTERS: If a fish is identifiable as a clupeomorph, how might it further be identified as an anchovy? The skeleton shows at least two characters that are unique to anchovies (among clupeomorphs). One is the oblique (posterior) inclination of the suspensorium (fig. 2), and the other is that the mesethmoid bone projects in advance of the vomer (fig. 3) and supports a paired rostral organ (Nelson, 1984a).

These osteological characters have been noted by several taxonomists and make anchovies relatively easy to recognize even on the basis of external morphology (Ridewood, 1905; Whitehead, 1963).

INTERRELATIONSHIPS: Anchovies, traditionally grouped in one family, have been divided by Whitehead (1972) into two subfamilies, Coiliinae (including *Coilia*) and Engraulinae (including all other genera of anchovies). This division is based on the peculiarities of *Coilia* (fig. 3E), but not on any evidence that suggests the monophyly of Engraulinae (e.g., figs. 3A–D, F–H). Grande (1985) indicates that some Old World genera of Engraulinae are more closely related to *Coilia* than to other anchovies, and that the Engraulinae of Whitehead are a paraphyletic group.

Engraulis has been grouped with the New World anchovies (Engraulini of fig. 4) since Jordan and Seale (1926) on the basis of absence of scutes (save for the single pelvic). In fact, *Engraulis* seems most closely related to the genus *Cetengraulis* among the New World forms (Nelson, 1984b).

Nelson (1983) presented characters indicating that *Engraulis* (cosmopolitan distribution) and the New World anchovies (*Anchoa, Anchoviella, Anchovia, Cetengraulis, Lycengraulis, Pterengraulis*) plus *Encrasicholina* (=Indo-Pacific species of *Stolephorus,* in part) form a monophyletic group (Engraulinae of fig. 4). These characters include a unique arrangement (within Clupeomorpha) of sensory canals, the fusion of a toothplate to the first epibranchial, and in the caudal skeleton of adults a fusion between preural centrum 1 and ural centrum 1. To these characters Grande (1985) added the loss of the dorsal scute (also lost from some species of *Stolephorus*).

Further studies have shown that the Engraulinae have their nearest relatives in the restricted genus *Stolephorus,* and with them form the group Engraulidae (of fig. 4). The defining characters of this group include an oval egg, a nearly full spine on preural centrum 1, epurals reduced to two, the rear edge of hypurals 5–6 in line with the lower hypurals, first two predorsal bones in close proximity, fused ecto- and metapterygoid bones, and a gap in the tooth row of the dentary.

Some of the Old World genera appear to be related to *Coilia* (Grande, 1985). Like *Coilia,* the genera *Lycothrissa, Papuengraulis, Setipinna, Thrissina,* and *Thryssa* have all lost the peg on the proximal end of the uppermost ray of the lower caudal lobe (fig. 5). This peg, so far as known, occurs in all other clupeoids. The systematic implications

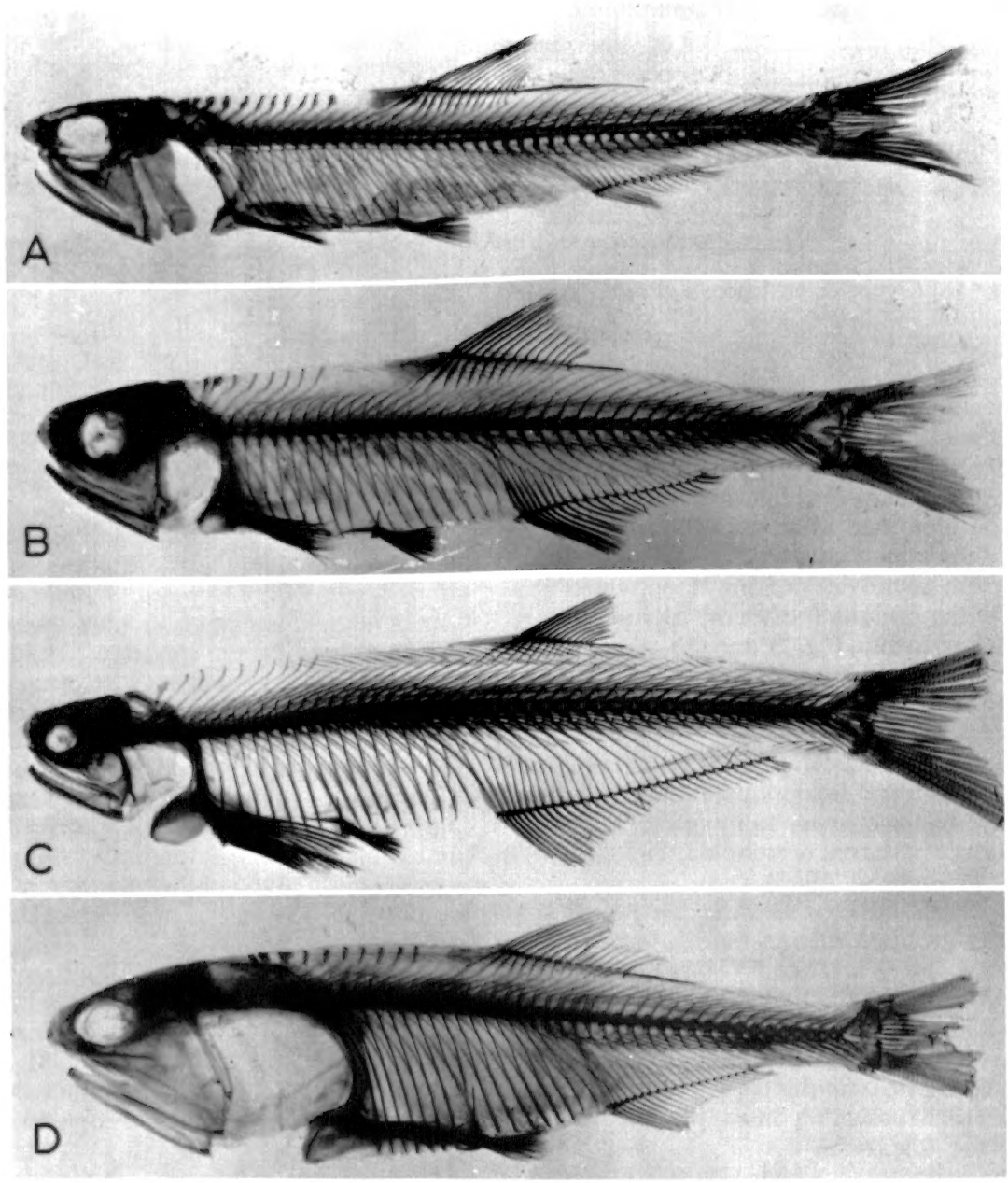

FIG. 3A–D. Cleared and stained anchovies (with hyobranchial apparatus and right cheek bones removed): (A) *Engraulis guineensis* (Rossignol and Blache, 1961), (AMNH 53904sw, sl = 68 mm) from the West African coast; (B) *Anchoviella lepidentostole* (Fowler, 1911), (AMNH 40905sw, sl = 65 mm) from Surinam: Nickerie District: Corintijn River; (C) *Pterengraulis atherinoides* (Linnaeus, 1758), (AMNH 48888sw, sl = 95 mm) from the Rio Orinoco, Venezuela; (D) *Cetengraulis mysticetus* (Gunther, 1866), (AMNH 42109sw, sl = 110 mm) from Pacheca Island, Panama.

of these possible relationships are depicted in figure 4, wherein these Old World genera are very tentatively grouped in the family Coiliidae (new usage).

FOSSIL ENGRAULOIDEA

The fossil species which have been referred to Engrauloidea can be divided into two categories of preservation. The first category in-

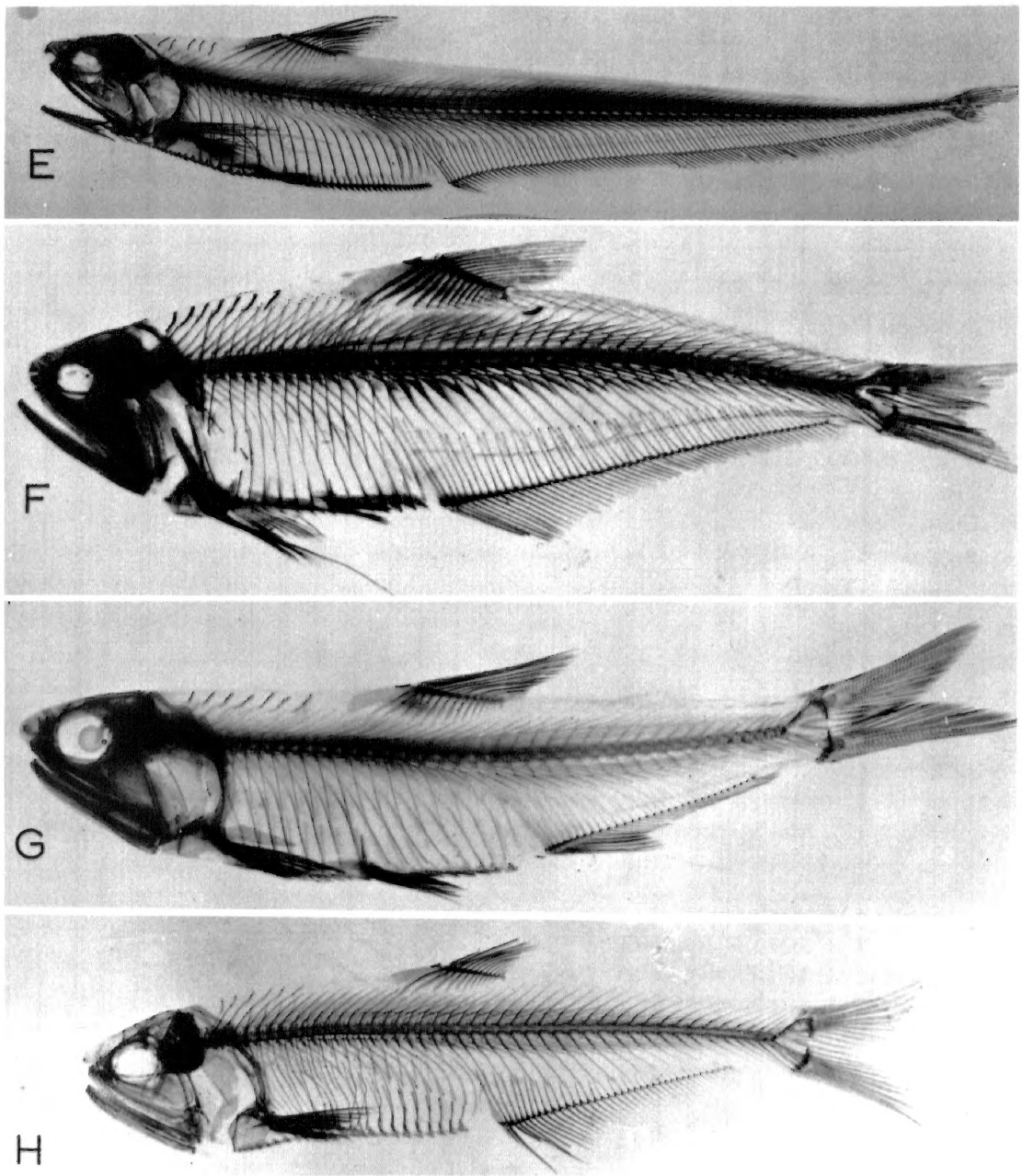

FIG. 3E–H. Cleared and stained anchovies (with hyobranchial apparatus and right cheek bones removed): (E) *Coilia rendahli* Jordan and Seale, 1926 (AMNH 10321sw, sl = 118 mm) from China: Hunan Province: Huping: Tungting Lake; (F) *Setipinna godavari* Baba Rao, 1961 (AMNH uncat., sl = 90 mm) from Papua New Guinea; (G) *Thrissina baelama* (Fôrskal, 1775), (AMNH 27026sw, sl = 104 mm) from a stream in Guam, west Pacific; (H) *Thryssa hamiltoni* (Gray, 1835), (USNM 217037, sl = 44 mm) from Papua New Guinea.

cludes those species known only by isolated otoliths. These species are tenuously assigned, so they will only briefly be mentioned below. The second category includes those species described on the basis of partial or complete skeletons. These species will be discussed in more detail.

The fossil species which have been de-

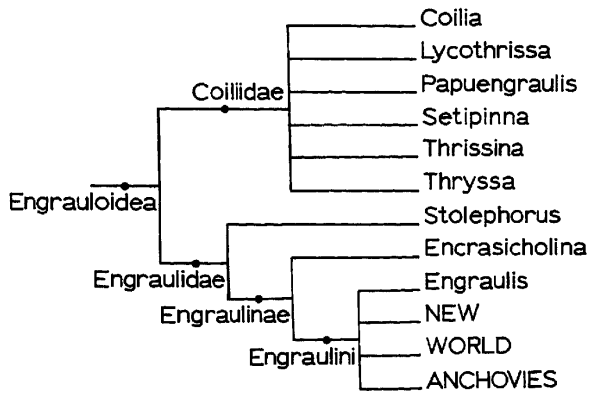

FIG. 4. Anchovy phylogeny, under the tentative assumption that the genera *Coilia, Lycothrissa,* etc., form a monophyletic group ("Coiliidae").

scribed as anchovies based only on isolated otoliths are:

†"*Coilia*" *planata* Stinton, 1962;
†"*Setipinna*" *retusa* Stinton, 1962;
†"*Stolephorus*" *productus* Stinton, 1977;
†"*Stolephorus*" *furculus* Stinton, 1977.

Stinton (1968) described †*Archengraulis productus* (in a monotypic genus) on the basis of Jurassic otoliths from southern England, and referred to the species as "a forerunner of the engraulids." Also, some yet unnamed anchovies have been reported on the basis of otoliths alone (e.g., †"*Setipinna*" sp. Stinton, 1977). We feel that there is insufficient information on teleost otoliths to warrant identification of the above species as anchovies, and we agree with Nolf (1982, p. 145) that "there are no valid otolith-based species [of Engrauloidea]." Several Plio-Pleistocene otoliths have been assigned to Recent engraulid species, including the following:

Anchoa compressa (Girard, 1858) [reported from the Pleistocene of California by Fitch, 1966].
Engraulis japonicus Schlegel, 1846 [reported from the Quaternary of Japan by Komiya, 1980].
Engraulis mordax Girard, 1854 [reported from the Pliocene of California by Fitch, 1967].

There are six fossil species represented by early complete skeletons which have previously been assigned to Engrauloidea. Of these, only one appears to be an anchovy. These fossils (discussed in detail below) include:

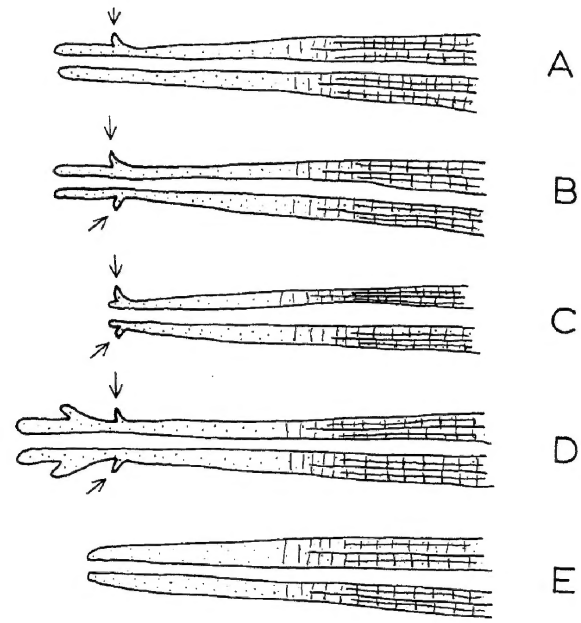

FIG. 5. The bases of the two middle caudal fin rays showing the dorsal and ventral "pegs" (arrows). Among all clupeoid species observed here, only *Setipinna, Lycothrissa, Papuengraulis, Thrissina, Coilia* and *Thryssa* (all Old World anchovies) have lost the ventral peg (A). Other anchovies, most clupeines, pellonulines and all alosines and dorosomatines, have a two-peg arrangement resembling B. Pristigasterids have a two-peg arrangement like B or C. Chirocentrids look like D and dussumieriines have a somewhat variable condition ranging from B (sometimes with the pegs pointing in a more medial direction) to C (sometimes with the pegs very poorly developed in some specimens). *Denticeps* (E) is representative of the non-clupeoid condition. Taken from Grande (1985).

†"*Engraulis*" *evolans* (Blainville, 1818) [Eocene marine deposits of Monte Bolca, Italy];
†"*Engraulis*" *brevipinnis* Heckel, 1853 [Middle Oligocene marine deposits of Chiavon, Italy];
†"*Engraulis*" *longipinnis* Heckel, 1853 [Middle Oligocene marine deposits of Chiavon, Italy];
†*Engraulis macrocephalus* Landini and Menesini, 1978 [from Plio-Pleistocene marine deposits of Calabria, Italy];

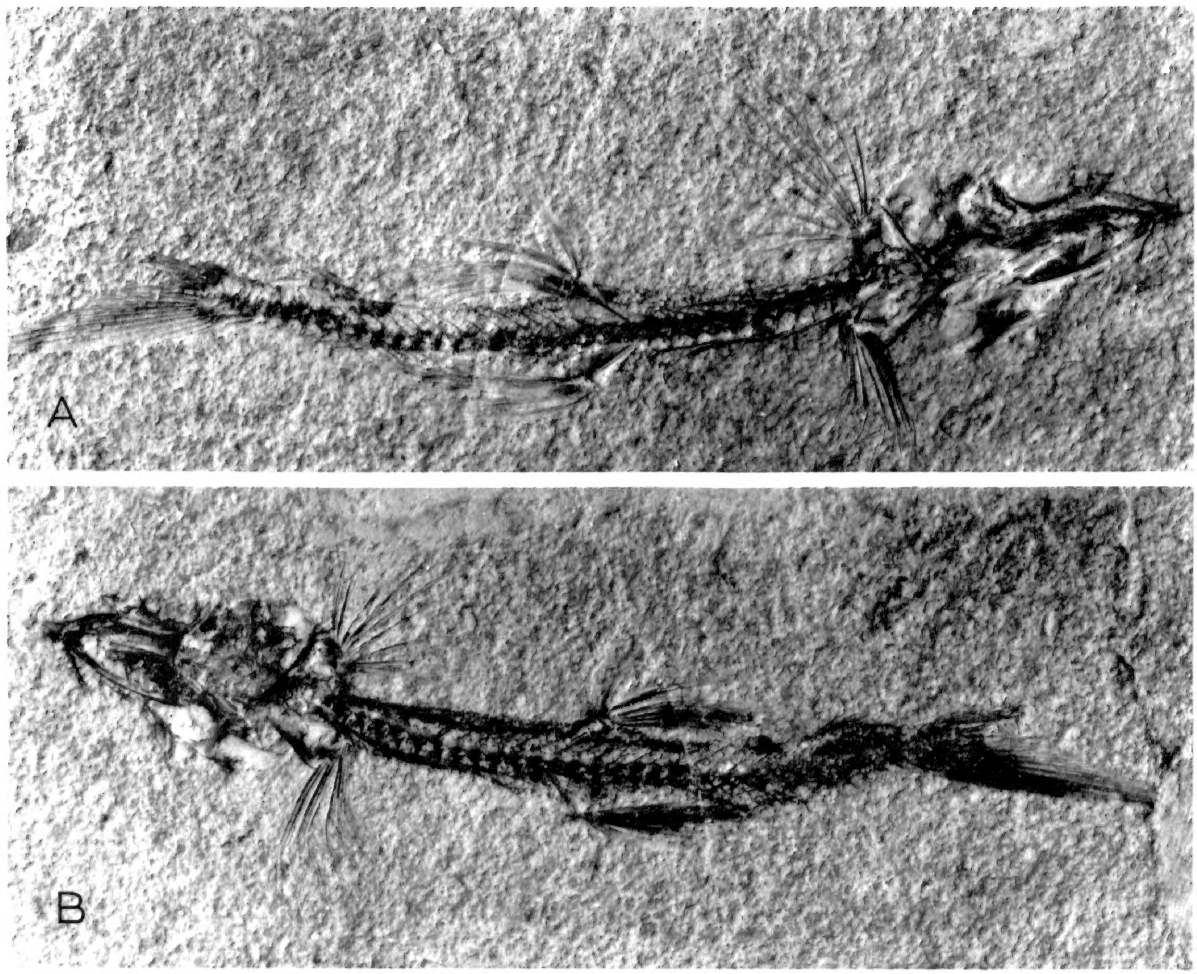

FIG. 6. †"*Engraulis*" *evolans* = †"*Clupea*" *evolans* Blainville, 1818; from the Eocene Monte Bolca deposits of Italy. Holotype, part and counterpart (A = MNHN 10944 and B = MNHN 10945); sl = 70 mm). Specimens first illustrated by Agassiz, 1833–1842: vol. 5, pl. 37b, figs. 1 and 2.

†"*Engraulites*" *remifer* Jordan and Gilbert, 1925 [Upper Miocene marine deposits of Lompoc, California];

†"*Stolephorus*" *lemoinei* (Arambourg, 1927) [from Miocene marine deposits of Oran, northern Africa].

Only one of the above species (†*Engraulis macrocephalus*) belongs in Engrauloidea. These six species will be discussed below, and a new species of fossil anchovy will be described.

The oldest fossil still occasionally referred to Engrauloidea is †*Clupea evolans* Blainville 1818, from the Eocene Monte Bolca Formation of Italy. Agassiz (1833–1842) was the first to place this species in the genus *Engraulis*. Jordan (1925, p. 12) and Jordan and Seale (1926, p. 393) questioned the validity of placing this species in Engrauloidea, but Blot (1980, p. 352), Danil'chenko (1964, p. 615), Romer (1971), and others still retained it in that group (Blot, p. 352, mistakenly cites Volta as author of the Blainville name). The type and only known specimen of †"*E.*" *evolans* (fig. 6) was examined and found not to be an anchovy. This specimen shows none of the characters derived for Engrauloidea (or even for Clupeomorpha), and the caudal skeleton (fig. 7) indicates that the fish is probably an exocoetoid (Jordan, 1925, p. 12 also suggested that this fish was "perhaps a young flying fish"). Therefore, there are no true anchovies known from Eocene (or earlier) time.

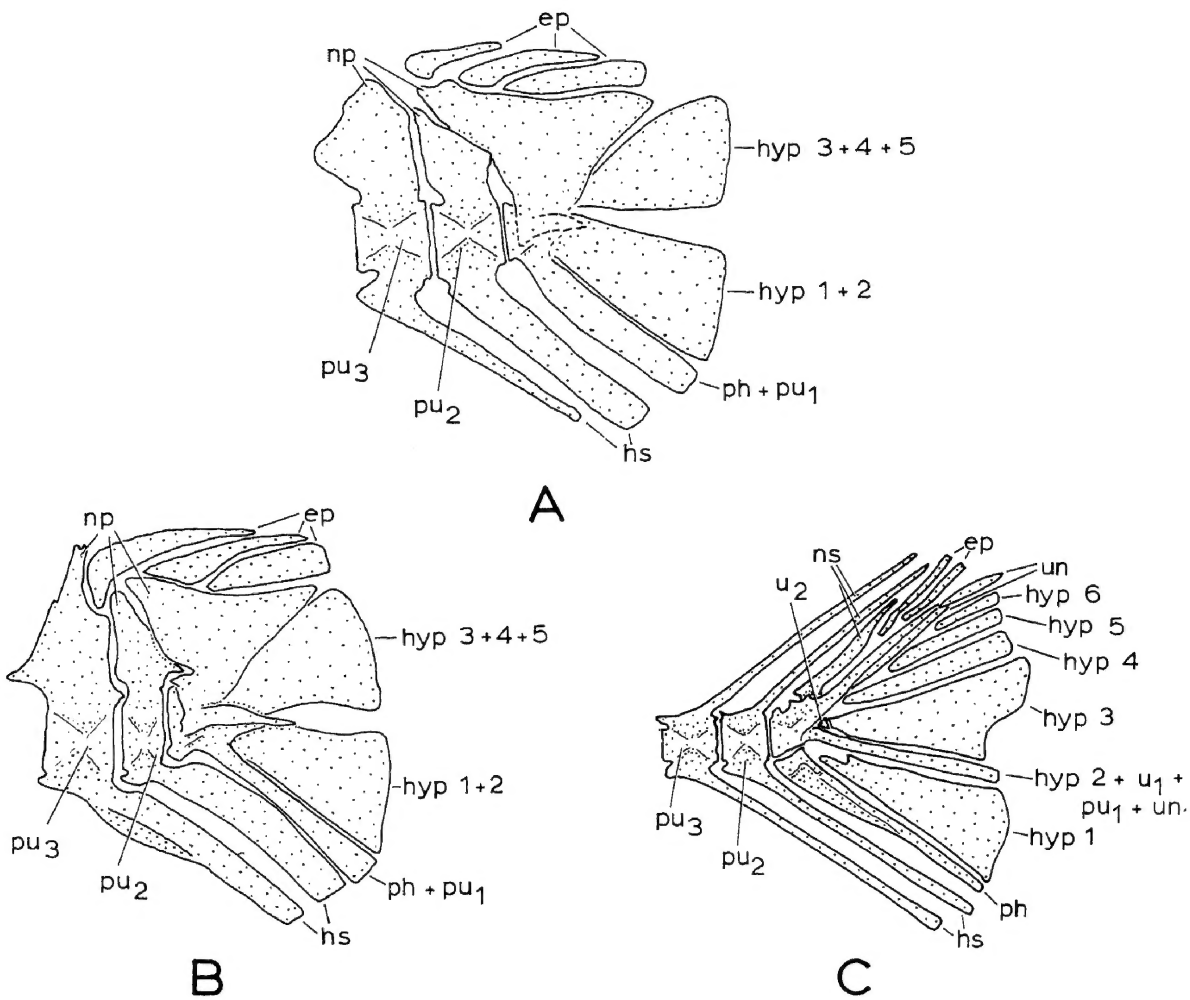

FIG. 7. Caudal skeletons of (A) †"*Engraulis*" *evolans,* drawn from part and counterpart of holotype specimen illustrated in figure 6 (dashed lines represent areas insufficiently preserved for accurate reconstruction); (B) *Exocoetus volitans* (an exocoetoid), drawn after figure 545 of Monod, 1968; and (C) *Pterengraulis atherinoides* (an engrauline anchovy) drawn from specimen in figure 3C. †"*Engraulis*" *evolans* is apparently an exocoetoid rather than an anchovy.

†*Engraulis brevipinnis* Heckel, 1853, and †*Engraulis longipinnis* Heckel, 1853, were both described from Middle Oligocene deposits at Chiavon (Chiavenna) in northern Italy. Jordan and Seale (1926, p. 375) put †*E. longipinnis* into the genus *Scutengraulis,* and commented (p. 356) that the relationships of †*E. brevipinnis* "seem not far from *Engraulis*"; but their assessment of these two fossil species was based solely on the original descriptions, which were brief and without illustrations. The type and figured specimens for the two Chiavon species are illustrated in figure 8. In our opinion, neither of these species belongs in Engrauloidea. †"*Engraulis*" *brevipinnis* (fig. 8A–D) shows no characters that would warrant its placement in Clupeomorpha (sensu Grande, 1985). No ventral scutes were observed, and the skulls of the specimens are badly crushed. This species has a peculiar arrangement of anal pterygiophores: all eight of these long slender bones converge proximally between a pair of haemal spines. Although some dussumieriines also have converging anal pterygiophores (e.g., *Etrumens teres,* AMNH 54603sw), the degree of convergence is not as great as in †"*E.*" *brevipinnis.* We doubt that †"*E.*" *brevipinnis* is a clupeomorph.

†*Engraulis longipinnis* (fig. 8E) has a series

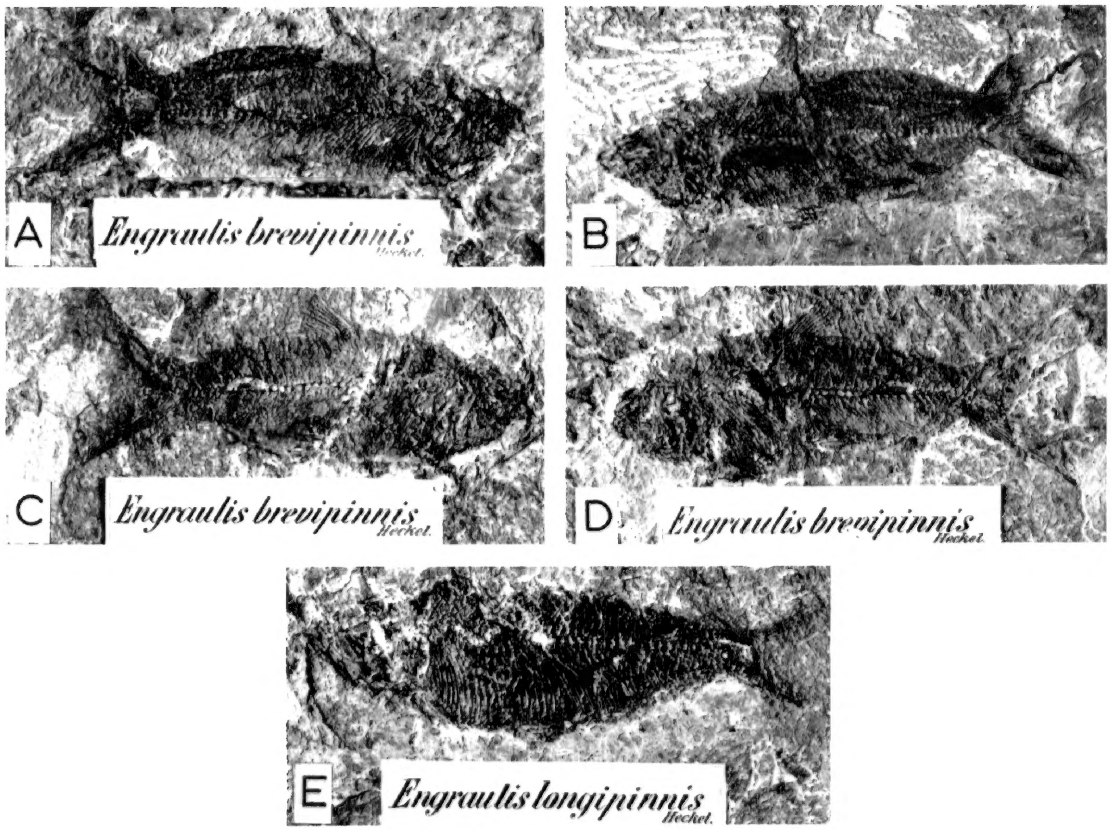

FIG. 8. Two species of fishes from Oligocene deposits of Chiavon, Italy, which were previously thought to be anchovies: †"*Engraulis*" *brevipinnis* Heckel, 1853 (A–D) and †"*Engraulis*" *longipinnis* Heckel, 1853 (E). A and B are part and counterpart (NMWGPA 3334 and 3325, sl = 13 cm) of syntype (designated by Heckel) for †"*Engraulis*" *brevipinnis*; C and D are part and counterpart (NMWGPA 3336 and 3327; sl = 13 cm) of second syntype (designated by Heckel) for †"*Engraulis*" *longipinnis* Heckel.

of ventral scutes indicating it is a clupeomorph, but it does not have a posteriorly inclined suspensorium, and in our opinion is a clupeid.

†*Engraulis macrocephalus* Landini and Menesini, 1978, was described from the Plio-Pleistocene marine deposits of the Vrica Section, Calabria, Italy. This species (originally described as a new subspecies of *E. encrasicolus*) is the only valid fossil engraulid species known to us, other than the new species we describe below. On the basis of the description, it appears to belong in the genus *Engraulis,* as described. The type description includes illustrations of seven nearly complete skeletons.

The monotypic genus †*Engraulites,* containing †*E. remifer* Jordan and Gilbert, 1925, was originally described as an engraulid (in Jordan, 1925). The type and only known specimen (fig. 9) consists of a small, poorly preserved anterior half of a fish from the Miocene deposit of diatoms at Lompoc, California. David (1943, p. 96), after close examination of the specimen, found it "undoubtedly belongs to the myctophid genus *Lampanyctus* Bonaparte, of which numerous specimens have been found in the California Miocene since the description of Jordan and Gilbert." We have examined the specimen and agree with David that it is not an anchovy. It is interesting to note that, of the tens of thousands of fossil fishes from Lompoc and other Miocene deposits of southern California, there are no known anchovies.

†*Spratelloides lemoinei* Arambourg, 1927, from Miocene marine deposits of Oran, northern Africa, was erroneously placed into the genus *Stolephorus* by Andelković (1969, p. 134). The type and figured material for this

FIG. 9. †*Engraulites remifer* Jordan and Gilbert (in Jordan, 1925) from the Miocene deposits of Lompoc, southern California. Known only by this single partial specimen (holotype CAS SU 651; total length of specimen = about 4.5 cm). This species, originally described as an anchovy, was found to be a myctophid by David, 1943. Although we do not necessarily consider the species to be in Myctophidae, we agree that it is not an anchovy.

species (illustrated in Arambourg, 1927, pl. 5, figs. 1–8) were all examined by Grande at MNHN, and this species clearly shows dussumieriin and spratelloidin characters (discussed in Grande, 1985) and does not show any characters diagnostic of anchovies.

In summary, there is probably only one described fossil species which belongs in Engrauloidea, †*Engraulis macrocephalus* Landini and Menesini, 1978, from the Plio-Pleistocene of Italy. The only other true anchovy fossils observed by the authors, after examining the fossil fish collections of FMNH, AMNH, USNM, BMNH, MNHN, and elsewhere, were several individuals of an undescribed Miocene fossil species from Cyprus, which will be described below.

Where are all the fossil anchovies? The scarcity of fossil anchovies has been noted previously by Whitehead (1963, p. 748). Anchovies should be at least as old (phylogenetically) as clupeids, according to all clupeomorph classifications observed here (see above). Fossil clupeids have a fossil record which extends at least as far back as Middle Paleocene[3] (Grande, 1982), and nominal fossil clupeid species are quite abundant from Paleocene to Recent time. Grande (1985) lists well over 100 nominal fossil species of Clupeidae known by articulated skeletons (3 Paleocene spp.; 9 Eocene spp.; 28 Oligocene spp.; 75 Miocene spp.; and 9 Plio-Pleistocene spp.); and there are over 150 Recent species. Considering the abundance and diversity of anchovies today (130 species), why is their fossil record so poor when compared to Clupeidae?

We propose that the reason for the scarcity of fossil fishes recognizable as anchovies is primarily an ecological one. Recent anchovies are mostly near-shore marine fishes, with some species entering rivers and streams. Most Cenozoic marine fossil localities which contain abundant well preserved articulated fishes are deposited in deeper water. To be identified to Engrauloidea (or to any other clupeomorph subgroup), a fossil must be reasonably complete and articulated (bones still in anatomical connection). Near-shore marine, river, and stream deposits, because of greater energy during deposition, are less likely to preserve articulated skeletons of fishes (especially those with delicate skeletons such as clupeoids) than lacustrine and deep-water marine deposits. Recent marine clupeids are not so confined to near-shore habitats and, unlike anchovies, clupeids have many lacustrine species. (Many of the fossil clupeids are from lacustrine deposits.) David (1943) gave a similar explanation for the absence of anchovy fossils in the tremendously fossiliferous deposits of the California Miocene. She noted (p. 96), "Fossilization did not occur in all the ecologic zones of the Miocene sea, for most of the fossil fishes found in California were deposited in rather deep water. This fact might explain why the Engrauloidea . . . inhabitants of shallower water, have not been found in the Miocene fauna." Therefore, because anchovy habitats appear to be much more restrictive than those of clupeids, and the anchovy habitats are in a relatively high-energy environment (=lower probability of fossilization), the relative scarcity of recognizable fossil anchovies is not so surprising. Restrictive habitats in life, and/or lack of adequate preservation for identification, are probably responsible for much of the incompleteness in the fossil record of various fish

[3] Other clupeomorph fossils such as †*Diplomystus*, †*Ellimmichthys*, †*Scombroclupea*, †*Gastroclupea*, etc., date back to the Cretaceous, but these are not clupeids; hey are more primitive forms (Grande, 1982, 1985).

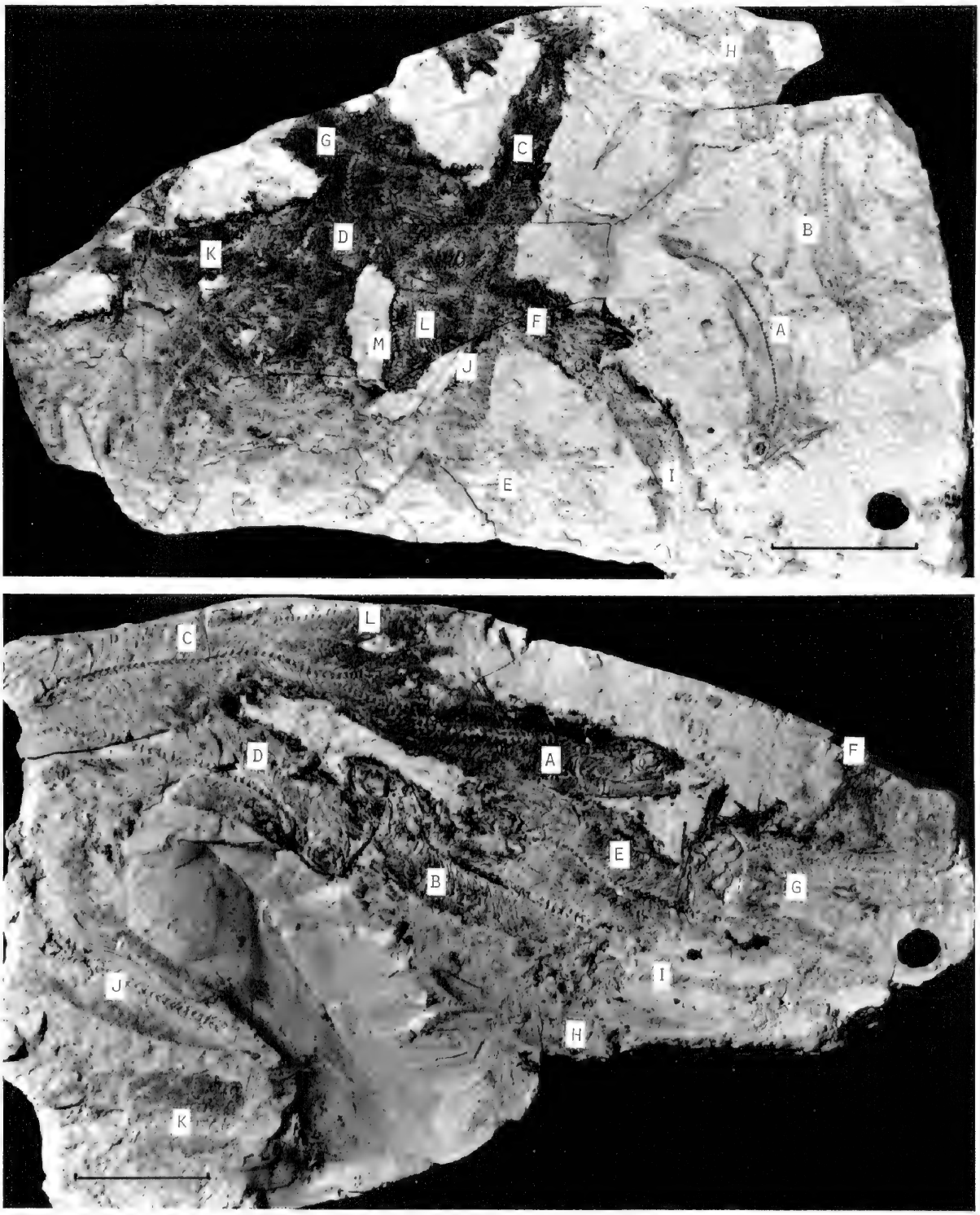

FIG. 10. †*Engraulis tethensis* n. sp. from Upper Miocene sediments of Cyprus. Holotype and paratypes: BMNH P.61224b.A–M (top) and BMNH P.61224a.A–L (bottom). Scale = 3 cm.

taxa (for example, no known coelacanthiforms between Cretaceous time and Present, no known petromyzoniforms between Pennsylvanian and Present, etc.).

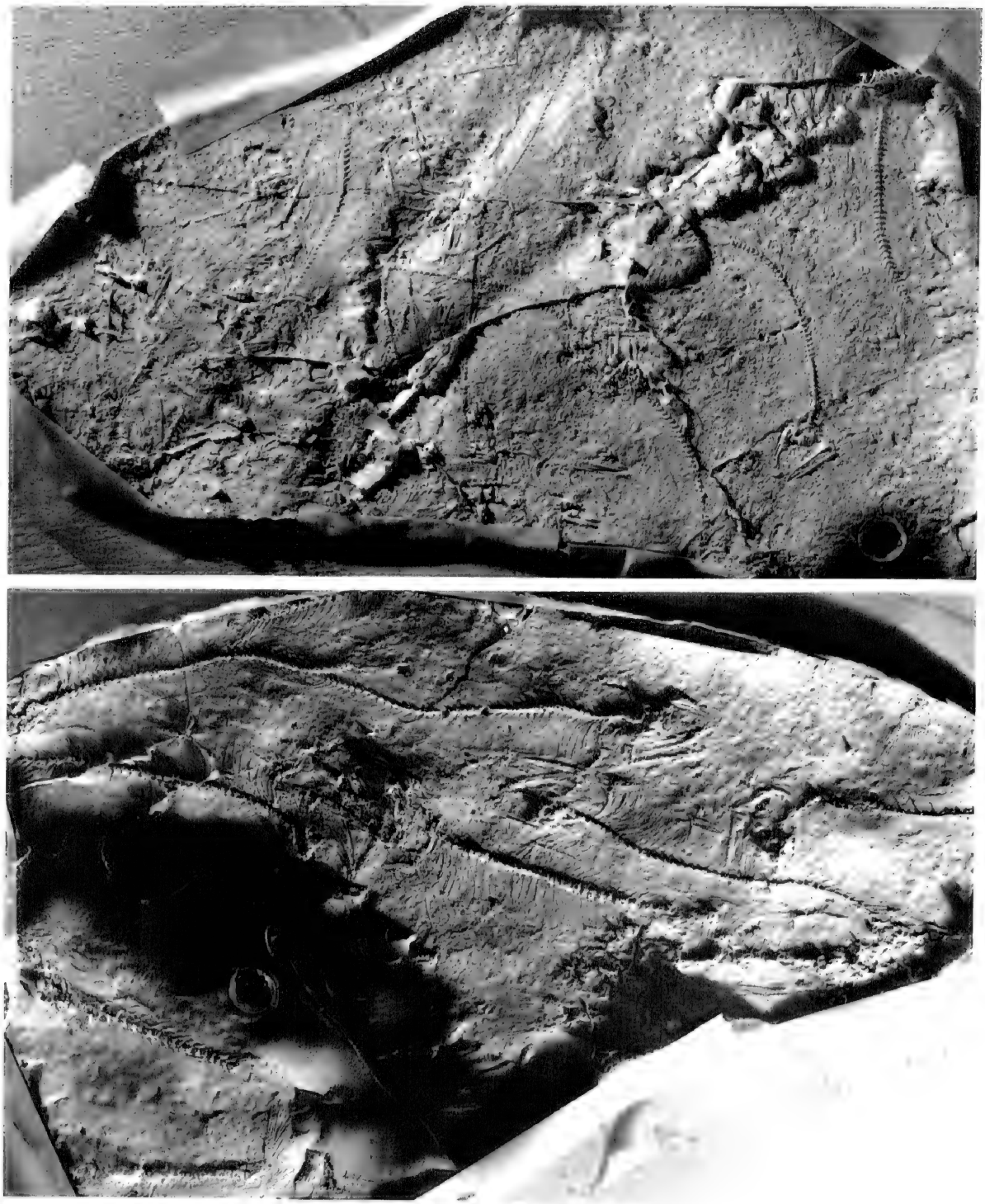

FIG. 11. †*Engraulis tethensis* n. sp. from Upper Miocene sediments of Cyprus. Latex peels of slabs in figure 10 (photographic negative reversed).

Recently a slab was deposited at the BMNH containing several individuals of an undescribed Miocene fossil species that is unquestionably referable to Engrauloidea. As explained above, other than the Plio-Pleistocene specimens from Calabria, Italy, these

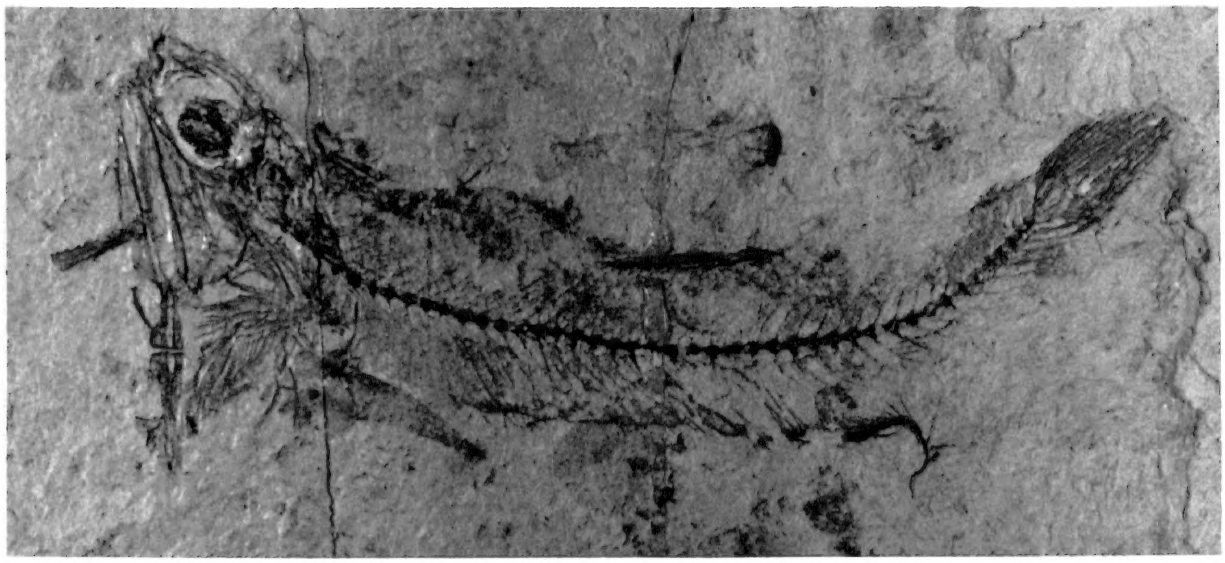

FIG. 12. †*Engraulis tethensis* n. sp. from Upper Miocene sediments of Cyprus. Holotype (BMNH P.61224b.A, sl = 59 mm).

specimens are the only known fossil anchovies. They all appear to belong to the same species, which will be described below.

†Engraulis tethensis n. sp. (figs. 10–12)

HOLOTYPE: BMNH P.61224b.A (fig. 12), a nearly complete fish preserved as an impression on a slab (figs. 10–11) with several other skeletons.

PARATYPES: BMNH P.61224b.B–M (figs. 10 and 11, top) and BMNH P.61224a.A–L (figs. 10 and 11, bottom); 24 partial to nearly complete skeletons preserved mostly as impressions in a soft, extremely fine-grained limestone.

REFERRED MATERIAL: BMNH P.61529.

LOCALITY: All three slabs are from Upper Miocene or Lower Pliocene sediments of the Mesaoria Group, in Lyssi (a village about midway between Nicosia and Famagust), Cyprus.

DIAGNOSIS: A species apparently quite similar to the Recent *E. encrasicolus,* but differing from it (and other species of *Engraulis*), most notably in having fewer vertebrae (cf. Nelson, 1984b).

ETYMOLOGY: *Tethensis* refers to the ancient geographic area (Tethys Sea) of origin of the species.

DESCRIPTION AND REMARKS: A moderate size anchovy with a known size range of 59–86 mm standard length (n = 5; $\bar{x}$ = 72.8). Measurements are given in table 1 and me-

TABLE 1

Measurements as Percentage of Standard Length for †*Engraulis tethensis* n. sp. (above) and *E. encrasicolus* (below)

	n	r	$\bar{x}$	S.D.
Body depth	4	17.5–20.1	18.6	1.173
	10	14.5–17.0	16.0	0.808
Head length	3	27.0–28.1	27.5	0.557
	10	26.3–28.1	27.3	0.563
Orbit diameter	5	8.1–9.3	8.6	0.507
	10	7.6–8.4	7.9	0.311
Eyeball diameter	3[a]	6.3–7.0	6.7	0.361
	10	6.2–7.0	6.7	0.209
Lower jaw length	5	17.4–21.2	19.4	1.434
	10	18.2–19.4	18.8	0.390
Dorsal fin base length	3	11.6–12.5	12.1	0.458
	10	11.2–13.0	12.1	0.614
Anal fin base length	1	15.0–—	—	—
	10	14.1–16.4	15.1	0.698
Prepectoral length	4	28.8–34.1	31.9	2.213
	10	26.4–28.2	27.5	0.590
Prepelvic length	3	49.4–52.6	50.7	1.701
	10	44.0–48.1	46.1	1.202
Predorsal length	4	50.8–54.3	52.5	1.780
	10	49.4–52.1	50.9	0.986
Preanal length	3	68.8–74.6	71.8	2.902
	10	64.7–66.7	66.7	1.391

[a] Based on preserved pigment.

TABLE 2
Meristics for †*Engraulis tethensis* n. sp. (above) and *E. encrasicolus* (below)

	n	r	x̄	S.D.
Dorsal pterygiophores	5	13–14	13.8	0.447
	20	13–16	14.2	0.716
Anal pterygiophores	3	16–18	17.0	1.000
	20	15–18	16.4	0.686
Pectoral finrays	2	15–16	15.5	0.707
	20	15–17	15.5	0.607
Pelvic finrays	2	7	—	—
	20	7	—	—
Caudal finrays	1	1, 9, 8, 1	—	—
	20	1, 9, 8, 1	—	—
Preural vertebrae	5[a]	42–43	42.2	0.447
	20	42–44	43.5	0.607
Predorsal bones	2	10–11	10.5	0.707
	20	10–11	10.4	0.510
Ventral scutes[b]	4	1	—	—
	20	1	—	—

[a] Specimen BMNH P.61224b.A shows 23 precaudal and 18 caudal vertebrae in contrast to *E. encrasicolus* (24–26 + 17–20 = 42–44).

[b] Pelvic scute only.

ristics in table 2. No dorsal scute. The single ventral (pelvic) scute has well-developed laterally ascending arms (well preserved on BMNH P.61224b.B). The first two predorsal bones are relatively close to each other, but all other predorsal bones are evenly spaced (well preserved on BMNH P.61224a.A). Premaxilla, maxilla, and dentary are finely toothed. One specimen (BMNH P.61224b.A) appears to show a small anterior gap in toothrow of the dentary (as noted for Recent *Engraulis* spp. by Whitehead, 1973, pp. 92–93). Dentary symphysis below vertical at midpoint between snout tip and anterior border of orbit. Two elongate supramaxilla. Posterior end of maxilla (well preserved on BMNH P.61224b.E) is blunt and rounded as illustrated for *Engraulis encrasicolus* in Whitehead (1973, fig. 30a). Snout slightly shorter than eye diameter. Anal fin insertion well behind vertical from last dorsal fin ray, and pelvics insert just in advance of dorsal fin. Caudal skeleton is indistinguishable from that of Recent *Engraulis* species. Scales thin, missing on several specimens; many are reticulate (well preserved on BMNH P.61224a.J–K).

†*Engraulis tethensis* is the oldest known valid fossil species of Engrauloidea. It is morphologically similar to the living European anchovy (*Engraulis encrasicolus*) in many respects, but differs mainly in having fewer vertebrae.

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